云南沾益早泥盆世肺鱼类一新种1)

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摘要:记述了云南沾益地区下泥盆统穿洞组肺鱼化石一新种——多脊混磨鱼(Tarachomylax multicostatus sp. nov.),归入标本包括一件左上齿板、一块 B 骨、一块可能是 3 骨的骨片和 6 个零散鳞片。主要特征:齿板内侧及后侧边缘被小齿(denticles)覆盖;齿脊 11-12 列,齿板中缘与最后一列齿脊夹角约 135°;内翼骨侧凹不明显,后侧部窄小呈尖状;B 骨和 J 骨上的前凹线沟相连;鳞片出露区与被覆压区之间有小齿瘤带。

关键词:云南,泥盆纪,肺鱼类

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1 前言

中国迄今发现的泥盆纪肺鱼有 5 属,分别是奇异鱼(Diabolepis)(Chang and Yu, 1984)、东山鱼(Dongshanodus)(王俊卿,1981)、吮吻鱼(Sorbitorhynchus)(Wang et al., 1990, 1993)、艾瑞克鱼(Erikia)(Chang and Wang, 1995)和掌双翼鱼(Chirodipterus)(Song and Chang, 1991)。此外,在江苏南京上泥盆统五通组中曾报道有双翼鱼科的鳞片(刘东生、潘江,1958)。

新的化石地点位于云南沾益县城西南约7km处的上双河村附近。该地区泥盆纪非海相地层发育,早泥盆世地层自下而上可划分为:西山村组、西屯组、桂家屯组、徐家冲组和穿洞组。穿洞组由黄绿、灰白色砂岩与粉砂岩组成(朱敏、王俊卿,1996),上覆海口组地层,下、中泥盆统界线在穿洞组与海口组之间或通过穿洞组顶部。新材料产于穿洞组下部灰白色砂岩中,与其伴生的鱼类化石有 Kenichthys campbelli 和 Heimenia sp. 等(Chang and Zhu, 1993;朱敏、王俊卿,1996)。依据孢子、鱼及双壳类等化石,化石层的时代可对比到埃姆斯期(刘振锋等,2004)。

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2 标本记述

硬骨鱼纲 Osteichthyes Huxley, 1880

肉鳍鱼亚纲 Sarcopterygii Romer, 1955

肺鱼目 Dipnoi Müller, 1844

混磨鱼属 Tarachomylax Barwick et al., 1997

多脊混磨鱼(新种) Tarachomylax multicostatus sp. nov.

(图1-4)

正型标本 一件不完整的左上齿板。中国科学院古脊椎动物与古人类研究所标本登记号:IVPP V 15041.1。

归入标本 一块 B 骨(IVPP V 15041.2)、一块可能是 3 骨的骨片(IVPP V 15041.3) 和 6 个零散鳞片(IVPP V 15041.4-9)。

词源 multi (La.), 多; costatus (La.), 有棱脊的。表示新种齿脊较多。

产地和时代 云南省曲靖市沾益县;穿洞组,早泥盆世埃姆斯期。

特征 齿板较大,内侧及后侧边缘被小齿覆盖。齿脊 11-12 列,呈放射状排列,中心点位于齿板中后部,齿板中缘与最后一列齿脊夹角约 135°。牙齿表面具珐琅质层。内翼骨侧凹不明显,后侧部窄小呈尖状。B 骨和 J 骨上的前凹线沟相连。B 骨前缘被覆压区较长。鳞片出露区和被覆压区之间覆盖有小齿。

描述 齿板 一件不完整的左内翼骨齿板,其前部缺失,后中部齿脊、台面及后侧部

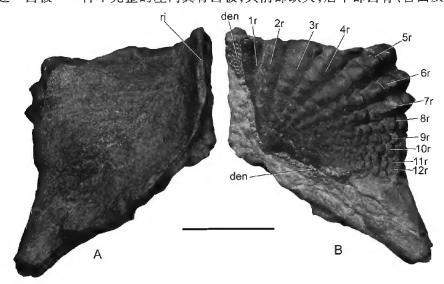


图 1 多脊混磨鱼(新种)的左内翼骨齿板(正型标本, IVPP V 15041.1)

Fig. I An incomplete left pterygoid tooth plate of *Tarachomylax multicostatus* sp. nov. (holotype, V 15041.1)

A. 背面 in dorsal view; B. 腹面 in ventral view; 比例尺 scale bar = 10 mm

简字说明 Abbreviations: 1r-12r. 1st-12rth tooth row 第 1-12 列齿脊; den. denticles 小齿; ri. ridge 脊

保存完好(图 18)。由于保存不完整,齿板整体长度未知,保存部分长 2.2 cm,宽 2.0 cm。齿板有 11-12 列齿脊,脊之间为沟,沟底未见小齿。由于齿板前部缺失,不能确定中央 4 列齿脊之间是否有小齿。第 1 列齿脊高而窄,只保存了后部,未见明显齿突。第 2-4 列齿脊均只保存了后部,较第 1 列宽平,牙齿已被严重磨蚀。第 4 列齿脊的侧端保存一不完整齿突。第 5-11 列齿脊保存完整且齿突清晰可见,齿脊高度依次递减,其中第 5 列为保存齿脊中的最长列,长 1.5 cm。第 5-7 列各有 3 个边界清晰的齿突,均以侧端者最大,向内逐次递减。齿突呈锥形,断面为等腰三角形。第 8-10 列齿突依次明显减小,每列可辨 4 个齿突,台面齿突已被磨蚀,隐约可见齿脊走向。第 11 列齿脊明显变窄,由 5 个形状不规则的齿突组成。第 11 列之后有两个不规则的小齿突,可能构成第 12 列齿脊。齿板近中缘处以及后侧边缘有不规则排列的小齿,但在齿板中后部拐角处未保存。齿板外侧与内翼骨后侧部平缓连接,没有类似双翼鱼(Dipterus)(White, 1965)的侧凹(图 3)。内翼骨后侧部窄小,末端变尖。

齿板背侧扇形,中心位于第5列齿脊的侧端。齿板中缘及中后边缘平缓连接呈弧形,边缘有一个高脊(ri,图1A),高度约5 mm。

B 骨 是一块两侧对称的长形骨片,长2.2 cm,宽1.2 cm,厚约0.1 cm (图2A,B)。其上呈倒"八"字形的凹线沟(前凹线沟)是辨认 B 骨的标志之一。骨片的主要部分呈七边形,被两条韦氏线(wl1, wl2)分成三个区域(z1-3,图2A,B)。靠中央的区域(z1,z2)被整列层覆盖。靠外围的区域(z3)表面粗糙,仅在两侧各有一个整列层覆盖的"小痘"(bli,

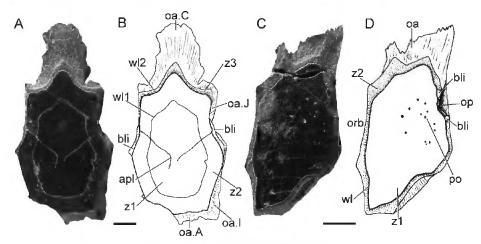


图 2 多脊混磨鱼(新种)颅顶甲骨片

Fig. 2 Skull-roof bones of Tarachomylax multicostatus sp. nov.

A, B. B 骨 B bone(V 15041.2); C, D. ?3 骨 a possible 3 bone (V 15041.3)

比例尺 scale bars: A, B = 2 mm; C, D = 5 mm

简字说明 Abbreviations: apl. anterior pit line 前凹线沟; bli. blister covered with cosmine 整列层覆盖的 "小痘"; oa. overlapped area 被覆压区; oa. A, oa. C, oa. I, oa. J. overlapped areas by A, C, I, J bones 被 A 骨、C 骨、I 骨、J 骨覆压区域; op. opening for supraorbital sensory canaliculus 眶上感觉管分支开口; po. pores for supraorbital sensory canal 眶上感觉管开口; orb. orbital margin 眶缘; wl, wl1, wl2. Westoll-line 韦氏线; z1-3. Zone 1-3 of cosmine 整列层区域 1-3

图 2A, B),说明该区域可能正处于整列层形成期。前部约相当于骨片长度 1/4 的部分及骨片周边的狭长地带有放射状纹饰,为被覆压区。参照肺鱼颅顶甲骨片的一般结构,B骨前部区域应为成对的 C 骨覆压,包括当中较宽长的部分,以及侧边的两个短小的前突;B骨两侧狭长地带为 J 骨和 I 骨覆压,后部为 A 骨覆压。前凹线沟向前延伸至 B 骨边缘,估计应与 J 骨上的前凹线沟相连。

? 3 骨 一块零散保存的骨片,长1.5 cm,宽0.7 cm(图2C,D)。骨片主要部分(区域1,z1,图2C,D)被整列层覆盖,表面有不规则排列的感觉孔(po,图2C,D),但仅局限于骨片右部。区域1周围有一个几乎不具整列层的条带(z2,图2C,D),仅右侧条带处有两个直径不到1 mm的整列层"小痘"(bli),说明该区域可能与上述 B 骨的区域 3 相似(z3,图2A,B),正处于整列层形成期。

骨片前侧和右侧边缘有被覆压区(oa,图 2C,D),但左侧边缘未见覆压区或被覆压区,可能是眼眶边缘,因此该骨片大致应属于围眶骨系列。从骨片的内侧面看,在两个"小痘"中间有一水平穿入骨片的小孔(op,图 2C,D),代表感觉管的位置。但在骨片周边见

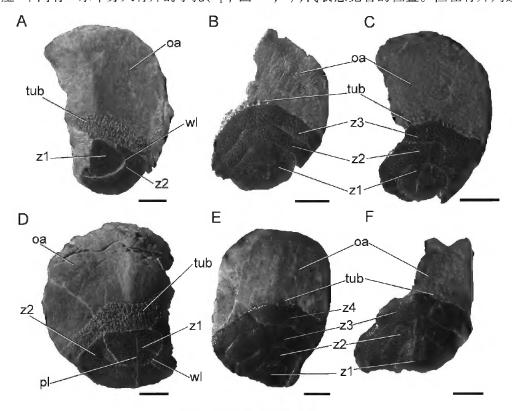


图 3 多脊混磨鱼(新种)零散鳞片

Fig. 3 Isolated scales of Tarachomylax multicostatus sp. nov.

A. V 15041.5; B. V 15041.8; C. V 15041.7; D. V 15041.4; E. V 15041.6; F. V 15041.9 比例尺 scale bars; A, D = 5 mm; B, C, E, F = 2 mm

简字说明 Abbreviations; oa. overlapped area 被覆压区; pl. pit line 凹线沟; tub. tubercles 小齿瘤; wl. Westoll-line 韦氏线; 21-4. Zone 1-4 of cosmine 整列层区域 1-4

不到另一开口,说明该感觉管在骨片内部终止,可能属于主侧线管的某一旁支末端。这和骨片表面的感觉孔分布也是一致的。综合上面两种判断,我们认为该骨片可能为3骨。 考虑到肺鱼头部骨骼的变化较大,以上只能作为一种推测。

鳞片 同层位发现的还有 6 个不完整的零散肺鱼类鳞片(IVPP V 15041.4-9)。6 个鳞片分两种不同类型(图 3),测量数据见表 1。

鳞片 V 15041.4 和 V15041.5 相似(图 3A,D),较大,完整鳞片应近圆形。鳞片前部及前侧部较大的区域是被相邻鳞片覆盖的区域,表面粗糙。其后为一弧形小齿瘤带,小齿呈锥形,齿的中部略凹陷,齿尖指向后方,并向后方倾斜。仅鳞片后部较小的椭圆形区域由整列层覆盖,其上仅见一条与鳞片后缘和侧缘平行的韦氏线。韦氏线与整列层区域前缘相交。鳞片 V 15041.4 上可见一凹线沟(图 3D)。

鳞片 V 15041.6-9 较前两鳞片小(表1;图 3B, C, E, F)。前部为被周围鳞片覆盖的区域,后部为由整列层覆盖的椭圆形出露区,其上见 2-3 条韦氏线。韦氏线前部与侧部均与出露区边缘平行,并伸达后部。最内圈韦氏线的后部与鳞片后缘重合。整列层区与覆盖区之间只有一列小齿瘤。

就最先形成的整列层区域(z1,图3)的相对位置而言,两类鳞片明显不同。大鳞片的区域1与小齿瘤带相接,而小鳞片的区域1位于鳞片的后端。这说明它们有着不同的生长方式,这种差异不太可能是由于生长期不同所致,而可能是由于生长部位的不同。通过与 Ørvig (1969a,图3,4)提到的肺鱼鳞片排列方式与分布状况比较,我们推测两类鳞片中较大的两个可能为腹侧中线两侧的鳞片或侧线鳞,较小鳞片可能是鳍部鳞。

表 1 多脊混磨鱼(新种)鳞片测量
Table 1 Measurements of scales of Tarachomylax multicostatus sp. nov. (cm)

标本编号 Scales	V 15041.4	V 15041.5	V 15041.6	V 15041.7	V 15041.8	V 15041.9
最大长度 Maximum length	3.0	3.0	1.2	0.9	0.9	0.8
最大高度 Maximum depth	2.0	2.1	0.9	0.6	0.6	0.8
出露区最大长度 Maximum length of exposed area	1.0	1.0	0.7	0.5	0.5	0.4
出露区长度/最大长度 Ratio between maximum length of exposed area and total length	0.33	0.33	0.58	0.56	0.56	0.50
小齿瘤带宽度 Width of tubercle band	0.5	0.5	< 0.1	< 0.1	< 0.1	< 0.1
韦氏线条数 Number of Westoll-lines	1	1	3	2	2	2

3 比较与讨论

由于上述肺鱼类材料发现于同一地点的同一层位,颅顶甲骨片与鳞片表面的整列层、 韦氏线结构一致,且个体大小相差不大,我们暂把它们归入同一属种。新材料与肺鱼类中 的混磨鱼和双翼鱼属很相近,但是与混磨鱼相似的特征较多。

在最近的系统发育分析中,混磨鱼均处于比双翼鱼更低的演化级(Schultze, 2001; Ahlberg et al., 2006)。混磨鱼属以前仅有一种——欧氏混磨鱼(Tarachomylax oepiki)被描述。新材料与欧氏混磨鱼的齿板有许多相似处:齿板内侧及后侧边缘被小齿覆盖,内翼

骨侧凹不明显,后侧部窄小,后端变尖(图4),因此我们将新材料归入混磨鱼属。

但是新材料又有一些特征与欧氏混磨鱼明显区别:新材料齿脊有 11-12 列,而欧氏混磨鱼的齿脊只有 7-8 列;新材料齿板中缘与最后一列齿脊夹角约 135°,而欧氏混磨鱼中该夹角小于 90°;新材料齿板较大,而欧氏混磨鱼齿板长度小于 1 cm (Barwick et al., 1997)(图 4);新材料前凹线沟在 B 骨和 J 骨上相连,而欧氏混磨鱼的前凹线沟则在两个骨片上断开。鉴于新材料与欧氏混磨鱼的相似处和明显区别,我们建立了一新种——多脊混磨鱼(Tarachomylax multicostatus sp. nov.)。

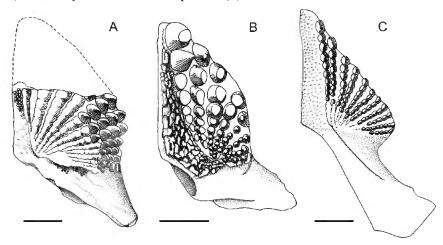


图 4 多脊混磨鱼(新种)(A)、欧氏混磨鱼(B)和瓦氏双翼鱼(C)内翼骨齿板比较

Fig. 4 Pterygoid tooth plates of Tarachomylax multicostatus sp. nov. (A), Tarachomylax oepiki Barwick et al. (B), after Barwick et al., 1997, fig. 8.2, and Dipterus valenciennesi Sedgwick & Murchison (C), after White, 1965, fig. 50, and Bernacsek, 1977, fig. 12D

比例尺 scale bars: A, C = 10 mm; B = 5 mm

此外,新材料与双翼鱼也有一些相近的特征,例如齿脊数目、齿板中缘与最后一列齿脊夹角、齿板大小和 B 骨整体形状(White, 1965; Den Blaauwen et al., 2005)等。但是,新种与双翼鱼又有很多区别:双翼鱼齿板内侧被"整列层"覆盖,新种齿板内侧被小齿覆盖;双翼鱼齿板外侧有明显侧凹,新种齿板外侧平缓;双翼鱼内翼骨后侧部较宽阔,且延伸较长,新种内翼骨后侧部则相对窄小(图4)。考虑到齿板内侧有"整列层"为双翼鱼的一个重要鉴定特征,我们认为不应该把该类群归人双翼鱼属。

混磨鱼属的模式种——欧氏混磨鱼发现于俄罗斯北地群岛,时代为早泥盆世埃姆斯期。与新材料的发现地点相似,在欧氏混磨鱼发现处也有 Heimenia 伴生,说明两个地点的地层可以对比,所以我们推测华南板块和俄罗斯北地群岛在埃姆斯期可能曾存在某种古地理联系。

与混磨鱼相似的双翼鱼分布在苏格兰(Forster-Cooper, 1937; Westoll, 1949)、北美西岸(Perkins, 1971)、澳大利亚东南部(Long and Turner, 1984)、德国和俄罗斯(Obruchev, 1940; Gross, 1964)等地的中晚泥盆世地层中。混磨鱼和双翼鱼属的发现地点沿古大洋两岸分布,可能再次印证了早泥盆世肉鳍鱼类演化跨古大洋的分布格局(朱敏、赵文金, 2006)。

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A NEW SPECIES OF DIPNOI (SARCOPTERYGII, OSTEICHTHYES) FROM LOWER DEVONIAN OF YUNNAN, CHINA

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Key words Yunnan, China; Devonian; dipnoan

Summary

A new dipnoan, Tarachomylax multicostatus sp. nov. is described from the Chuandong Formation (late Emsian, Lower Devonian) of Yunnan Province, South China. It represents the sixth dipnoan genus from the Devonian of China. The other five genera are Diabolepis (Chang and Yu, 1984), Dongshanodus (Wang, 1981) and Erikia (Chang and Wang, 1995) from Yunnan, Sorbitorhynchus (Wang et al., 1990, 1993) from Guangxi, and Chirodipterus (Song and Chang, 1991) from Hunan.

The associated early vertebrates include *Kenichthys campbelli*, *Heimenia* sp. (Chang and Zhu, 1993; Zhu and Wang, 1996) and an undescribed antiarch.

1 Systematic paleontology

Dipnomorpha Ahlberg, 1991 Dipnoi Müller, 1844 Tarachomylax Barwick et al., 1997 Tarachomylax multicostatus sp. nov. (Figs. 1-4)

Etymology "multi" (La.), many, "costatus" (La.), with ridges, referring to the large number of tooth rows in the new form.

Holotype A left pterygoid tooth plate (IVPP V 15041.1).

Referred specimens Two skull-roof bones (B bone, IVPP V 15041.2; ? 3 bone, IVPP V 15041.3), and six isolated scales (IVPP V 15041.4-9).

Locality and horizon Zhanyi, eastern Yunnan, China; Chuandong Formation; Emsian, Early Devonian.

Diagnosis Large tooth plate with 11-12 tooth rows; plate surface between the most mesial tooth row and the median suture covered with denticles; posterior edge of the tooth-bearing surface with a few denticles; angle between the mesial edge of tooth plate and the last tooth row about 135°; "wing" of pterygoid narrow and short, with a pointed end; anterior pit line on B bone connected to the pit line on J bone; overlapped area on scales with a band of tubercles adjacent to the cosmine-covered surface.

Description Tooth plate The pterygoid tooth plate (IVPP V 15041.1) has not preserved its anterior part, and is about 2.2 cm in length. The total length of tooth plate should be much larger than that of *Tarachomylax oepiki* (Figs. 1, 4). The tooth-bearing surface is fan-shaped with up to 12 straight tooth rows, all radiating from a point situated posteromedially. The cusps are round and pointed anteriorly or laterally, and worn-out to form smooth ridges posteromedially.

The furrows separating tooth rows bear no tubercles, and are shallower between the more posterolateral tooth rows. The first tooth row is partly preserved, with the newly-formed teeth

missing. The preserved part is narrow and high, and comprises teeth which are strongly worn-out yet show cusp boundaries. The 2^{nd} – 4^{th} rows have also lost their anterior parts. The 5^{th} – 12^{th} rows are complete, and the teeth in each row become progressively larger laterally. The lingual parts of these rows are strongly worn out as in the more mesial rows. The plate surface between the first row and the median suture is covered with denticles, as in *T. oepiki* (Barwick et al., 1997). The posterior edge of the tooth-bearing surface also bears a few denticles. The "wing" of pterygoid is short and narrow when compared with that of *Dipterus* (Figs. 1B, 4). Unlike *Dipterus* which has a deep embayment on the lateral edge of pterygoid (White, 1965), the new form has a mildly-embayed lateral edge of pterygoid.

The tooth plate is fan-shaped in dorsal view, with the center at the lateral point of row 5. The mesial and posterior edges converge mildly and form an arch-shaped ridge (ri, Fig. 1A).

B bone The B bone is a symmetrical bone with the length of 2.2 cm, the width of 1.2 cm and the depth of 0.1 cm (Figs. 2A, B). The main part of the B bone is heptagon-shaped, and divided into three zones (z1-3, Figs. 2A, B) by two Westoll-lines (wl1, wl2, Figs. 2A, B). Zones 1 and 2 are cosmine-covered, and encircled by a narrow ring (z3, Figs. 2A, B) which is deficient of cosmine except for two blisters (bli, Figs. 2A, B). The presence of the blisters might indicate the forming of cosmine on the outermost zone. The overlapped areas of the B bone exhibit radiating striations, and consist of a long anterior part and a narrow ring around the main part. The anterior part should be the overlapped areas by paired C bones, the lateral part by I and J bones and the posterior part by A bone (Figs. 2A, B). The shape of B bone and the overlapped area by I bone suggest that I bones are separated by B bone posteriorly. The anterior pit lines extend to the lateral edges of B bone, suggesting that they are connected to the anterior pit lines on J bones.

?3 bone The possible 3 bone has the length of 1.5 cm and the width of 0.7 cm (Figs. 2C, D). The main part (zone 1, zl, Figs. 2C, D) is covered with cosmine, and carries several pores (po, Figs. 2C, D) of the supraorbital canaliculus. Around Zone 1 is a narrow ring with two small cosmine blisters (bli, Figs. 2C, D), which is similar to Zone 3 of B bone. A foramen (op, Figs. 2C, D) is situated between the two blisters in lateral view, and serves as an exit for the supraorbital canaliculus. The canaliculus possibly terminates in this bone since no other exit for the canaliculus is visible and pores of the sensory canaliculus are restricted to the right part of the cosmine area. Thus this bone should not belong to the main lateral line series, but possibly to the series lateral to it. The overlapped areas are visible along the anterior, right and posterior margins. However, no overlapped area is present along the left margin of the bone, which possibly represents the orbital margin. Accordingly, we assign this bone as a possible 3 bone.

Scales Six rounded scales with Westoll-lines can be classified into two types (Fig. 3). The first type includes the scales V 15041.4 (Fig. 3D) and V 15041.5 (Fig. 3A), which are bigger and thicker than the others. The anterior and anterolateral parts of the scale are the area overlapped by neighboring scales (oa, Figs. 3A, D), and have a series of pores similar to T. oepiki (Barwick et al., 1997). Posteriorly, the scale bears a wide tubercle band (tub, Figs. 3A, D). Each tubercle has a distinctive shape with a high crested ridge around the posterior edge, a "spoon-shaped" concave superficial surface as in Heimenia (Ørvig, 1969b) and an anterior edge that merges into the surrounding bone. The scales of first type carries only one Westoll-line (wl, Figs. 3A, D) on their exposed surface, with the earliest formed cosmine area (zl, Figs. 3A, D) adjacent to the tubercle band.

By comparison, the scales of the second type are distinctively small and thin (V 15041.6-9, Figs. 3B, C, E, F). They have a narrow tubercle band, but 2 or 3 Westoll-lines on their exposed surface, with Zone 1 situating posteriorly and away from the tubercle band.

Comparing with the scales figured by Ørvig (1969a, figs. 3, 4), we assume the scales of the first type situating on the ventral side along the midline or from the main lateral line and

those of the second type presumably from fins.

2 Comparison and discussion

All referred specimens were collected from the same bed and the same site as the holotype. They are compatible in size, and have the same cosmine and Westoll-line structure. Among the known dipnoans, the specimens described here most resemble *Tarachomylax* and *Dipterus*.

Although we have not reached a consensus regarding the lungfish phylogeny, most of the analyses suggest the pre-Dipterus level of Tarachomylax (Schultze, 2001; Ahlberg et al., 2006). Only one species of Tarachomylax — the type species T. oepiki has been described so far. New specimens resemble T. oepiki in the following characters: tooth plate surface between the first tooth row and the median suture covered with denticles; "wing" of the pterygoid narrow and short; embayment at the lateral margin of pterygoid not developed (Fig. 4); overlapped areas of scales with a tubercle band adjacent to the cosmine-covered surface, and a band of distinctively porous bone anterior to the tubercle band (Barwick et al., 1997).

T. multicostatus can be distinguished from T. oepiki by the following characters: large tooth plate with 11-12 tooth rows; angle between the mesial edge of tooth plate and last tooth row about 135°; anterior pit line on B bone connected to the pit line on J bone; cosmine on scales without distinct ridge pattern. For all these reasons we refer the Zhanyi specimens to Tarachomylax, and name it a new species of that genus, T. multicostatus.

The new species also shows many similarities with *Dipterus* in the size of tooth plate, the number of tooth rows, the angle between the first and last tooth rows, the shape of B bone, and the anterior pit line connected on B bone and J bone (White, 1965). However, it differs from *Dipterus* in several important aspects: no cosmine-like material present on the surface of tooth plate; the "wing" of the pterygoid short and narrow; embayment absent at the lateral margin of the tooth plate (Fig. 4); tubercles present on scales (Forster-Cooper, 1937). Considering the diagnostic character of cosmine-like material on the tooth plate in *Dipterus*, we do not assign this new form to *Dipterus*.

The type species of *Tarachomylax* is found from the Emsian of Severnaya Zemlya (Siberian Arctic), in association with *Heimenia* scales (Barwick et al., 1997). In Zhanyi, the new species of *Tarachomylax* is also found together with *Heimenia* scales. The similarities between the two strata suggest that the South China Block and Severnaya Zemlya might have some paleogeographic connections during the Emsian. The genus *Dipterus* which is very similar to *Tarachomylax*, is known from the Middle and Late Devonian of Britain (Forster-Cooper, 1937; Westoll, 1949), Germany and Russia (Obruchev, 1940; Gross, 1964), North America (Perkins, 1971) and southeastern Australia (Long and Turner, 1984). Both these two genera are distributed along the Panthalassic Ocean, supporting the trans-Panthalassic Ocean distribution pattern of early sarcopterygians (Zhu and Zhao, 2006).

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